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Contractor: Cornell University, Section of Ecology & Systematics

Principal Investigator: William N. McFarland, Cornell University

Co-Principal Investigator: Sanford Moss (last year contract).

Title of Project: A study of the effect of group metabolism on the schooling behavior of fishes.

Objectives: Objectives of the study were manifold, but can be considered under two categories (1) Field objectives and (2) Experimental verification. Both approaches were designed to determine if group metabolism was sufficient to effect school structure and behavior.

Format: This final report is submitted as a reprint of one published paper dealing with objective (1) above and as a xerox copy of a manuscript being submitted for publication that deals with objective (2) above.

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THE INFLUENCE OF DISSOLVED OXYGEN AND CARBON DIOXIDE ON FISH
SCHOOLING BEHAVIOR

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Dense schools of marine fish such as northern anchovies (Engraulis mordax), Atlantic menhaden (Brevoortia tyrannus) and striped mullet (Mugil cephalus) have been observed by us in various formations which can change kalaidoscopically in minutes or seconds. These changes in shape often may be accompanied by changes in the direction of school movement. This variability in school structure appears to result from seemingly random alterations in the behavior of individuals or perhaps small groups within the school.

In a recent publication we described changes in school structure and considered factors that might alter the behavior of fish within a school (McFarland and Moss, 1967). Of the various factors considered, oxygen and carbon dioxide seemed labile enough to warrant investigation. Field investigation revealed that the concentration of these gases could be drastically altered by the presence of a school of fish. These findings provided a basis for a hypothesis which relates some aspects of school behavior to school metabolism. According to this hypothesis environmental concentrations of these gases are altered within dense groups of schooling fish as a result of the metabolism of the included individuals. These changed parameters (increased P_{CO_2} , decreased P_{O_2}) are sensed by individual fish within the

school. The detection of reduced O_2 and/or increased CO_2 acts to modify swimming behavior in such a way as to minimize the potential impact of metabolism on the group. The sum of the behavioral modifications so produced results, according to the hypothesis, in the continuously changing internal structure of fish schools often noted by ourselves and others (Breder, 1959; 1965; Thompson, 1955; 1966; Whitely, 1945; 1946; Eibl-Eibesfeldt, 1962; Shaw and Tucker, 1965).

In addition to respiratory gas concentrations other features of the external and genetic environments may operate as sources of the observed behavior. Organic substances of intra or interspecific origin such as "Schreckstoff"-like chemicals may result in behavioral modification. Certainly various innate or learned behavior patterns may result in the observed school modification. In particular, Shaw and Tucker (1965) have stressed that slight variations in swimming speed of a type seen in schooling fishes may be normal features of their behavior and may result in circulation of individuals through a school. In spite of the alternative possibilities our hypothesis remains plausible since respiratory gases, particularly oxygen, are altered within schools of striped mullet in nature. Moreover, these depletions of environmental oxygen are similar to those expected on the basis of metabolic calculations. Finally, behaviors were observed in dense schools which were interpreted as resulting from severe metabolic reductions in environmental oxygen (McFarland and Moss, 1967).

Further development of our hypothesis depends on the demonstration that schooling fishes sense and respond to alterations in respiratory gas concentrations of magnitudes actually measured in the field. Several authors have investigated and demonstrated that both behavior and physiology in a

wide variety of fishes can be modified by environmental changes in oxygen and carbon dioxide (Bull, 1940; Collins, 1952; Jones, 1952; Harden-Jones, 1960; Alabaster and Robertson, 1961; van Sommers, 1962). Little information, however, is available on the effect of these gases on schooling behavior. Several pertinent questions can be posed. What effect does lowered oxygen have on schooling behavior? What effect does increased carbon dioxide have on schooling behavior? Are there differences in behavioral responses of schools when gas levels are changed either acutely or chronically? What quantitative changes in oxygen and carbon dioxide concentrations are needed to induce significant behavioral changes in a fish school? Our attempts to obtain this information provides an experimental test of our hypothesis and forms the basis of the present communication.

Methods:

The experiments described here were conducted during the summers of 1964 and 1965 at the Scripps Institution of Oceanography, University of California at San Diego. The northern anchovy (Engraulis mordax) was chosen as the experimental animal because of its strong predilection toward schooling.

Live anchovies were obtained from stocks maintained in nearby Mission Bay. Only apparently healthy fish were selected. These were brailled into tubs of well oxygenated water, transported to the laboratory and placed in large circular tanks supplied with a constant flow of sea water. Transport time averaged twenty minutes and little mortality resulted. The fish usually were held for 24 hours, but never more than 48 hours. The mean standard length of anchovies used was 12.2 cm (range 11.0 to 13.2 cm).

Fish were used in only one experiment and discarded.

Apparatus: The experimental tank was a circular galvanized stock tank, 100 cm in diameter and 50 cm deep. It was coated internally with light green resin. Water was circulated with a plastic centrifugal pump with suction connected at the side drain located 2.5 cm above the tank bottom. The pump discharged into a 120-liter plastic reservoir. Water was recirculated from this reservoir through siphons and created a counter clockwise current in the main tank. After several trials the main tank water level was adjusted to a depth of 14 cm and recirculated at a rate of 30 liters/minute. The turnover rate was 17.2% of the tank volume (tank volume = 174 liters; reservoir volume = 70 liters). Average surface peripheral current under these conditions was 7m/minute. The current velocity in the first quadrant downstream from the siphon outlets was fastest and declined to its slowest value in the fourth quadrant near the suction outlets. Velocity of the water in the inner 75 cm of the tank was quite slow. Aeration was provided in the reservoir tank above the level of the siphon intakes. In this way entrainment of gas bubbles in the water flowing into the main tank, which could distort school behavior, was avoided. To serve as a means of introducing water of various oxygen or carbon dioxide concentrations, a second 130-liter reservoir was provided which could be emptied into the reservoir containing the siphons. Water of low oxygen level was produced by scavenging with nitrogen. High oxygen levels were produced by adding medical oxygen. Low pH was produced by gassing the second reservoir with carbon dioxide. The second reservoir, which always contained 70 liters of pretreated water, was introduced into the first reservoir by gravity flow. This required two minutes and produced a flow of 35 liters per minute or slightly in excess of the normal circulation rate

of the pump. In order to maintain a relative balance in flows the discharge of the pump during this two-minute period was directed from the primary reservoir to drain and then returned. The additional flow of 5 liters per minute was removed by a series of overflow holes around the periphery of the main tank located 14 cm from the bottom.

Fluorescent and incandescent overhead lighting was located outside the periphery of the tank. To eliminate visual disturbance a black plastic screen was placed around the tank during experiments.

Oxygen concentrations were measured with a Precision Scientific Galvanic Cell Analyzer and by standard Winkler technique. Temperature in degrees centigrade was measured with a thermistor. Records of school movements and positions were made with a remotely controlled movie camera mounted 8 feet directly above the tank.

Indices: To evaluate the effects experimental procedures might have had on schools of anchovies confined within the tank, it was necessary to convert the photographic data into numerical form. Two indices were chosen which provided information on the two major spatial aspects of fish schools: density (compactness) and polarization parallel (orientation). We identify these indices as the mean distance from the center of the school (M.D.C.S.) and the orientation angle ($Or.\angle$). They are defined and calculated as follows:

(1) M.D.C.S. A single photographic record of the position and orientation of a school of fish was projected onto a white surface with a black dot located at its center. About this dot were a series of concentric circles separated by spaces equivalent to 3 cm. The central dot was placed at the center of the school. The distance of each fish was recorded from it. From

this data the mean distance of an individual fish from the center of the school was calculated.

(2) Orientation angle. From a single record an imaginary line was drawn through the head and trunk of each fish in the school. The angle between the intersection of the imaginary lines of two fish which were nearest neighbors was assigned a number from 0 to 4 as follows: 0 = angle less than 22.5° ; 1 = angle between 22.5° and 67.5° ; 2 = angle between 67.5° and 112.5° ; 3 = angle between 112.5° and 157.5° ; and 4 = angle between 157.5° and 202.5° . This number was called the orientation number and represents the angle between two fish to the nearest 45 degrees. For instance, two fish oriented at right angles to each other were each assigned a value of 2, whereas two fish facing opposite to each other were each assigned a value of 4. When all fish in a school had been rated by orientation number the mean was calculated and converted into an orientation angle by multiplying by 45 degrees. The largest orientation angle possible would be 180° . Under this circumstance each closest pair of fish would be oriented to opposite directions. Where a school was swimming with all fish parallel the orientation angle would be zero degrees.

One advantage of this measurement, wherein nearest neighbors are used as an orientation parameter, is that highly polarized but turning and milling schools of fish will yield relatively low orientation angles. By using both M.D.C.S. and orientation angle ($Or.\angle$) the spacing within a school can be assessed independent of orientation and vice versa. The M.D.C.S. is similar to the mean separation distance indice used by Hunter (1966) for analysis of schooling behavior. The orientation angle, however, differs from Hunter's mean angular deviation indice since it emphasizes the polarization between

nearest neighbors rather than the orientation of the group.

Those experiments where the responses of anchovy schools to rapid changes of dissolved oxygen or carbon dioxide were tested the average swimming velocity of the school was estimated. This was done by projecting each frame of the motion picture film onto a white surface and placing a dot at the estimated geometric center of the school. The linear distance between successive dots was then divided by the elapsed time between frames to obtain the velocity estimate.

To determine how many anchovies to use in experimental studies the M.D.C.S. and the Or. \angle were determined as a function of numbers of fish in the experimental tank. Tests were run on groups containing 2, 3, 5, 10, 15 and 25 fish (Fig. 1). For our experiments on changed environmental gas levels, we chose to use schools of 10 and 15 anchovies. This was done because under normal conditions a low M.D.C.S. could be expected.

Results:

To determine if relatively long term or chronic changes in gas concentrations could effect behavioral changes in schooling fish, a series of experiments were run where either the dissolved oxygen or the pH (increased CO_2) were slowly reduced. Photographs were taken of the school at 15-second intervals during the entire length of the experiment (usually about 2 hours). The M.D.C.S. and the Or. \angle were calculated from ten pictures drawn from fifteen minute intervals. Examples of typical dissolved oxygen and pH chronic experiments are presented in Figures 2 and 3.

Significant changes in the M.D.C.S. were evident only when oxygen and carbon dioxide levels approached the lethal values for anchovies. Orientation

angle showed only a non-significant tendency to increase when these approached lethal values. In all experiments where environmental oxygen and carbon dioxide were changed gradually the integrity of school structure was maintained until lethal values were approached. In another set of experiments the average swimming velocities of anchovy schools were analyzed as a function of dissolved oxygen and pH. The O_2 or pH was lowered in a stepwise fashion. After each change to a new gas level the fish were allowed to adjust for 15 minutes and then movies were taken at 12 frames per second for one minute. The swimming velocities recorded by this procedure are given in Table I. In these experiments no notable increases in school swimming speeds could be demonstrated with either decreased pH or oxygen. Indeed, if any relationship exists mean school swimming speeds tended to decrease slightly at least through the initial reductions in these parameters.

A series of experiments were designed to test the hypothesis that rapid transitory changes of dissolved gases cause brief behavioral modifications of a sort that could not occur in chronic or long term experiments. In these "acute" experiments, rapid gas concentration changes were produced and school movements photographed at 12 frames per second. Swimming velocities were examined as a function of both dissolved oxygen and pH. The results of typical oxygen and pH experiments are given in Figure 4. The several experiments of each type that were run are summarized in Table II. Significant increases in mean swimming velocity of anchovy schools were produced by acute changes in both oxygen and carbon dioxide when compared with control periods in 9 out of 12 experiments. Where significant changes occurred, the swimming velocity usually increased by as much as two-to-three-fold. In the acute oxygen experiments the actual decreases in oxygen were within the range of changes measured within fish schools in nature. Changes in pH were considerably

greater than those detected within schools in nature. The maximum actual changes are indicated in Table II. In two experiments where oxygen was acutely increased rather than decreased (from 6.2 and 6.4 mg/l to 9.2 and 9.0 mg/l respectively) no significant change in swimming velocity could be demonstrated.

In contrast to the lack of behavioral changes shown by the groups of anchovies chronically exposed to low values of oxygen or high values of carbon dioxide, groups of anchovies transferred acutely into the identical conditions showed dramatic behavioral responses. These responses typically consisted of rapid swimming at the water surface, leaping from the water, absence of any schooling tendencies, and were followed within a minute or less by complete loss of equilibrium, convulsive-like gasping and death.

Discussion:

The behavior of anchovy schools exposed to slow reductions of dissolved oxygen or pH was remarkable in terms of its stability. That is, the size or density of the experimental school did not change significantly until dissolved oxygen values of less than 2 mg O_2 /l or pH values of less than 6.2 were experienced (Figs. 2 and 3). A similar stability was found with respect to orientation and swimming velocity (Figs. 2 and 3; Table I). To the observer the anchovies subjected to these conditions exhibited a gross physiological response well before apparent behavioral modification became manifest. Estimates of the ventilation rate (opercular movements per minute), for instance, demonstrated that this feature of the animal's physiology varied in a directly inverse fashion with reduction of either oxygen or pH. Thus, fish exposed to intermediate levels (say, 4 mg O_2 /liter, or pH = 7.0) exhibited

ventilation rate increases of 25 to 50 percent over initial values. Ultimately, behavioral modifications manifested by distress and change in school structure (Fig. 2 and 3) became apparent only slightly above lethal gas levels (LD_{50} for 2 hour exposure at $20^{\circ}C.$ = $1.0 \text{ mgO}_2/l$, or $pH = 6.1$). The results of these experiments do little to substantiate our hypothesis concerning the control of changes in school structure. They do, however, suggest that anchovies are behaviorally well adapted in that organization of the school would be maintained in environments subject to low levels of dissolved oxygen and pH.

Indeed many schooling fishes, including Engraulis mordax, commonly enter bays and estuaries where oxygen and carbon dioxide are subject to severe diurnal fluctuations. It would be interesting to compare the behavioral tolerance of pelagic schooling and non-schooling fish with respect to low oxygen and pH to test this idea more carefully. It would also be interesting to determine whether densely schooling species of fish like anchovies possess physiological adaptations for surviving in this kind of environment.

The method of analysis we have used in interpreting the results from the acute oxygen and pH experiments has resulted in a conservative estimate of the real response. The changes of swimming velocity exhibited by the experimental schools were transient and abrupt. The size of the experimental system limited the response in at least two ways. First, an individual fish avoiding a test gradient could turn and accelerate for only a very short period of time before having to brake for another turn. Second, it was apparent that frequently only the leading fish within a school would experience a test gradient. Its sudden avoidance of this gradient would turn the following fish before they reached it. These following fish moved more slowly in the direction of the leader(s), and succeeded in "catching up" without

markedly increasing their speed. As a result the mean velocity of the school was much lower than the actual velocity of the individual fish which reacted to the test gradient. Another conservative feature of the analytical method chosen was the use of rather large time intervals for averaging velocities for statistical purposes. For instance, a positive avoidance which could last five seconds or less could be hidden in data analyzed in 20 second intervals. In spite of these difficulties, however, the data presented in Table II indicate that statistically significant responses were elicited in all but three experiments. When the three apparently negative experiments are examined with respect to the three fastest school velocities in each statistical interval of 20 seconds, marked increases in the swimming speed can be correlated with declines in either dissolved oxygen or pH. This kind of analyses may be more indicative of the real response of the school because it does not mask the rapid but transient swimming velocities associated with response to the gradient.

Because the responses measured consisted of increases in swimming velocity in directions away from the experimental gradient, we consider them to be avoidances. This kind of avoidance behavior by schooling fish to decreases in oxygen and pH was predicted by our hypothesis. Avoidances of dissolved oxygen gradients as small as $-0.55 \text{ mgO}_2/\text{l}$ and pH declines on the order of 0.25 units occurred. These estimated gradients are the largest possible under the conditions of the experiments. Dilution of the introduced test water in the experimental tank probably reduced the real gradient which the anchovies actually experienced, but this was not measured.

The anchovies were found to avoid pH changes in excess of the kinds of variation we have actually measured in the field (McFarland and Moss, 1967).

We feel, however, that our failure to demonstrate avoidances to very small pH changes is due to our inability to measure accurately and control more precisely such slight changes (0.025 pH units). Positive avoidances to the levels of oxygen depletions normally measured through even small fish schools, however, are reported here. Thus, even in the absence of more precise data of the responses of schooling fish to changes of pH and/or CO₂, we feel the idea that schooling fish can avoid changes of respiratory gases is borne out.

The usual interval between the injection of treated water and a statistically significant response was on the order of twenty to thirty seconds (Fig. 4) or longer. This delay resulted from several factors. For example, the time of water movement from the treatment tank to the experimental tank; the response time of the oxygen analyzer and pH meter; the rate of movement of the introduced gradient within the system; and the time between introduction of the test gradient and the initial encounter of the fish school with it all provided a source of the observed time lag. Consequently, it is difficult to estimate with precision the length of the latent period between the initial encounter of the fish with the gradient and the avoidance response. Our subjective impression, however, was that this period was short and that the response elicited occurred due to the activation of a peripheral sensory system rather than due to a more deeply seated (and hence slower) physiological response. The suggestion here, then, is that in addition to the CO₂ or pH sensory system commonly assumed to exist in fish, a dissolved oxygen sensory system, perhaps located either externally or in the gills, may be present in these fish. Suggestion of a peripheral oxygen sensing system is not without precedence. Although responding to carbon dioxide, the chemoreceptive aortic and carotid bodies of mammals are more sensitive to oxygen (Comroe, 1964, 1965). The

effects from stimulation of these receptors are complex and variable, but distinct changes in cardiovascular and ventilatory function occur and, interestingly, increased activity of the motor cortex. Krogh (1941) indicated and this has been re-emphasized by Prosser and Brown (1961) that regulation of ventilation in air breathing forms is influenced mainly by carbon dioxide whereas in aquatic animals it is effected mainly by oxygen. Important in this respect is the suggestion by Schmidt (1938) that the oxygen sensitivity and carbon dioxide insensitivity of the carotid and aortic bodies might represent the evolutionary retention in mammals of an oxygen sensing system requisite to efficient gill ventilation in fishes. Certainly, a reflex relying on environmental oxygen would be more advantageous to a fish as compared to a mammal in controlling ventilation since, in general, oxygen fluctuates more and is less available in the aquatic than in the terrestrial environment. Carbon dioxide in natural waters is usually at a low concentration and as Krogh (1941) pointed out is not a regular stimulant to ventilation. But carbon dioxide like oxygen can have a pronounced effect on ventilation, as we have found for anchovies. Its action, however, could as well be on chemoreceptive areas of the medullary respiratory center as on peripheral cells. Koch (1931) postulated that the branchial arches of primitive vertebrates contain nerves and receptors for pressure reception. Chemoreceptive cells might also be associated with these pressure receptors (Schmidt and Comroe, 1940a). It is not unimportant to stress that the aortic and carotid bodies are associated closely with the pressoreceptors (aortic and carotid sinuses) which function in regulation of blood pressure in mammals. Comroe (1964) reviews the fact that chemoreceptor-like cells occur with the first, second, third, fourth and sixth aortic arches of mammals.

But a clear histological demonstration of chemoreceptive cells has not been forthcoming for teleosts (Mott, 1951). Pressoreceptor function occurs in the eel (Mott, 1951) and the dogfish (Lutz, 1930; Boyd, 1936). Anoxia produces vasoconstriction in the gill arterioles and also bradycardia in dogfish (Satchell, 1961, 1962) and the receptor sites seem to be located in the superficial portions of the gill. But their specific location and structure is unknown (Satchell, 1961). Given this background it seems plausible that peripheral oxygen receptors occur in the gill region of teleosts and effect changes in circulation, ventilation and quite likely behavioral responses as typified by avoidance reactions. A final point of interest concerns the broad similarities which result from a sufficient direct stimulation of the carotid body or its afferent nerve (Schmidt and Comroe, 1940b) and from acute exposure of anchovies to low environmental oxygen, namely an excited motor response which can reach convulsive levels.

The results of our observations and experiments convince us that densely schooling fishes like many non-schooling fishes are able to sense and avoid changes of dissolved oxygen and carbon dioxide (pH) normally produced within schools. Responses of this type, occurring within free swimming fish schools, can be responsible for modifications in school structure and behavior. As indicated earlier this aspect of school behavior may be considered adaptive in the sense that it allows all individuals to experience the advantage of being in a well oxygenated and normal pH environment an equivalent amount of time. But the actual changes in oxygen and carbon dioxide that occur within schools of fish are not sufficient to be lethal (typical reductions are from 2 to 20 percent for oxygen and 0 to 0.03 pH units, McFarland and Moss, 1967). The adaptive advantage of internal circulation and of avoidance of slight

reductions in oxygen and/or pH by individual members of a school requires, therefore, a more subtle interpretation. It is well known that chronic changes in respiratory gases lower active metabolism and the capacity of many fishes to sustain a constant swimming speed (Fry and Hart, 1948; Job, 1955; Basu, 1959; for review see Fry, 1957). The concept of "incipient limiting level" was introduced by Fry (1947) to emphasize the critical relationship between an environmental variable and the ability of a fish to maintain a level of activity appropriate to its survival. Of particular significance was the suggestion that any reduction in environmental oxygen which restricts the active metabolism of a fish, and as a consequence its capacity to behave, would be limiting and, therefore, unfavorable (Fry, 1957). Applying this concept and the demonstrated facts that reduced O_2 and increased CO_2 diminish the swimming capabilities and behavioral activities of a variety of fishes (Alabaster and Robertson, 1961; Jones, 1960; Katz, et al, 1959; Hubbs, et al, 1967; Fry, 1957) to a school of fishes the significance of internal circulation and avoidance of low O_2 and high CO_2 becomes apparent. Individual fish which did not avoid but remained in areas of low O_2 or high CO_2 content, which often occurs within fish schools, could be exposed to 'incipient limiting levels' of these gases. As a consequence their ability to be as active as other members of the school would be reduced. Certainly they would be more susceptible to predation. In addition, inability of these individuals to sustain higher levels of activity might lead to a decrease in the integrity of the school and its ultimate break-up. Or perhaps social stresses might result if the demands of group movement exceed the physiological capacity of these fish to move. A direct consequence of such stress would be an inefficient increase in the expenditure of energy

by the entire school. Internal circulation and avoidance behavior can be envisioned then as a means of decreasing the time of exposure to the environmental changes in O_2 and CO_2 that result from school metabolism. In effect this averages the resulting reduction in individual activity throughout all members of a school and, therefore, minimizes the disadvantageous consequences that may result from reduced activity. We wonder whether the suggested physiological necessity of having an adequate circulation of individuals through a school is related to the absence of hierarchy (Breder, 1959). Relationships which permit certain individuals to consistently assume favored positions might necessarily be disadvantageous to the school especially if gradients of critical features like respiratory gases helped define the favored positions. For instance, were dominant fish to occur within a school, subordinate individuals might be relegated more or less permanently to the physiologically less favorable internal and rearward positions containing reduced oxygen and increased pCO_2 . The school might be expected to reach a position where, lacking recruitment, only a few of the most dominant individuals survive. This, however, does not seem to occur, for the schooling group usually observed is large. In fact, the observation in recent years of spectacular population decreases of some schooling fishes (Sardinops sagax and Brevoortia tyrannus) may indicate that schools may have some minimum critical size which, when not met, places all individuals at a disadvantage. Densely schooling fishes seem to be nearly unique among social animals in not having apparent dominance hierarchies (Breder, 1959; Williams, 1964). This may, in fact, be one of the possible reasons for the recurrent observation that fish schools typically consist of similar sized individuals (Breder, 1959).

In the course of analyzing records of experimental anchovy schools, we

noted that the first fish to sense and respond to test gradients was not always the lead fish. This observation suggests to us that one function of the schooling habit may be the simple multiplication of available sensory systems. If all the individual sensory systems in a school are unequal in threshold sensitivity, it follows that for each sensory modality some individuals will be capable of finer discriminations than others. Such "perceptive" fish may well be relied upon (in a figurative sense) by others in the school to better escape predation, disadvantageous respiratory gas levels, or other potentially debilitating influences in the environment. At the present time we have no knowledge about the kind of physiological variation that may exist among the individual fish of a school. Moreover, we do not know if individual threshold sensitivity is constant or varies over time. Rather wide variation in the respiratory response of humans exposed to the same levels of oxygen has been reported, however, and the differences attributed from experimental data on dogs and cats to individual differences in the thresholds of the aortic and carotid bodies (Comroe, 1964).

One additional idea of general interest can be derived from the study. Although schooling fish occur in freshwater, reports of extremely dense and large schools similar to those seen in marine fish are not available. Although the quantification of schooling density and size has not been put on a comparative basis one obtains the impression that schooling fish do not form extremely large and compact schools in the freshwater environment. We wonder if this results from the lesser buffering capacity of freshwaters as compared to sea water. We suspect that if large schools as dense as those observed by us and others in the marine environment were to occur in freshwater, drastic pH declines would result from metabolic CO_2 release. Accord-

ingly, pH and/or pCO_2 may have important effects on the schooling behavior of freshwater fish. In an interesting paper in this regard, Shelbourn (1966) related increasing salinity with a greater tendency to aggregate in young chum salmon (Oncorhynchus keta). We suggest that this kind of effect also may be closely related to change in buffering capacity.

A natural phenomenon that may be related to this concept is the mass mortalities of alewives in the great lakes. The cause is unknown (Graham, 1956; Rothschild, 1966), but it is associated with a large increase in population size. Several hypotheses are prevalent and one suggests that population pressures cause the formation of schools of sufficient size to reduce environmental oxygen to lethal levels. We would extend this hypothesis to include increased carbon dioxide and reduced pH. Metabolically induced changes in Ph would be far greater in freshwater than would occur in similar schools of alewife in the marine habitat, although oxygen reductions presumably would be similar. Mass mortalities then might result as a consequence of the reduced buffer capacity of the habitat which allows the pCO_2 to reach levels where it directly and adversely effects the physiology of individual fish. It should be realized that these changes in pCO_2 and pH would potentiate the effects of reduced oxygen, and other adverse conditions such as increased temperature.

The formation of large dense schools in fresh-water, although necessary for effective breeding, is quite likely highly non-adaptive. Clearly more work in this regard is needed.

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TABLE I. The effect on swimming velocity of fish schools when exposed chronically to various levels of oxygen and pH. Fifteen minutes of exposure to each increment was allowed before collection of data. In each case N = 60.

Type Exposure	Oxygen (mg/l)	pH	Temp. °C	Mean Swimming Velocity + 2SE
pH	6.30	8.00	19.3	0.50 \pm 0.11
	6.20	6.70	19.4	0.34 \pm 0.16
	6.30	6.48	19.4	0.29 \pm 0.19
	6.20	6.30	19.5	0.44 \pm 0.18*
	6.15	6.10	19.6	0.00 ----**
O ₂	6.1	7.92	17.8	0.43 \pm 0.05
	4.6	7.92	17.8	0.34 \pm 0.18
	4.0	7.92	17.9	0.22 \pm 0.06†
	3.2	7.95	18.0	0.41 \pm 0.13
	2.4	7.95	18.1	0.37 \pm 0.09
	1.1	7.95	18.1	0.30 \pm 0.08††

* School showing loosening of Orientation. Or. \angle = 81° in some cases.

** School completely dispersed. All fish upside down.

† Swimming velocity significantly different from other values.

†† Group at times showing dispersion and signs of distress. Orientation decreasing but when schooled, fish maintain integrity and normal swimming velocity. Orientation \angle and M.D.C.S. at times very high.

TABLE 2. Summary of acute oxygen and carbon dioxide experiments.

<u>No.</u>	Dissolved Oxygen		
	Significant ^A increase in swimming velo- city of school following change	Three Fastest ^B of 20	Maximum O ₂ change
1	+	+	-0.55
2	+	+	-0.70
3	+	- ^C	-1.45
4	-	+	-1.70
5	+	+	-1.20
6	-	+	-1.30

pH (Increased carbon dioxide)			
<u>No.</u>	<u>Significance</u>	<u>Three Fastest</u>	<u>Maximum pH change</u>
7	+	+	-1.25
8	+	+	-1.30
9	+	+	-0.40
10	-	+	-0.25
11	+	+	-0.95
12	+	+	-0.80

A. (+) indicates an increase and no overlap between swimming velocities for 20 second post-control periods and control periods (based on 2 standard error of mean for samples of n=20).

B. (+) indicates that the three highest mean velocities during any twenty second interval exceeded all control velocities.

C. A noted increase occurred, but of the 60 velocities for the control period, one was unusually high, and overlaps with the three fastest following the control period. Note that significance exists for 20-second intervals.

Figure 1. Effect of numbers of the density and orientation of schooling anchovies.

Points represent the mean of 10 photographs of the appropriate school in the experimental tank (see text). M.D.C.S. is the mean distance from center of school and Or. \angle is the mean orientation between nearest neighbors within each school.

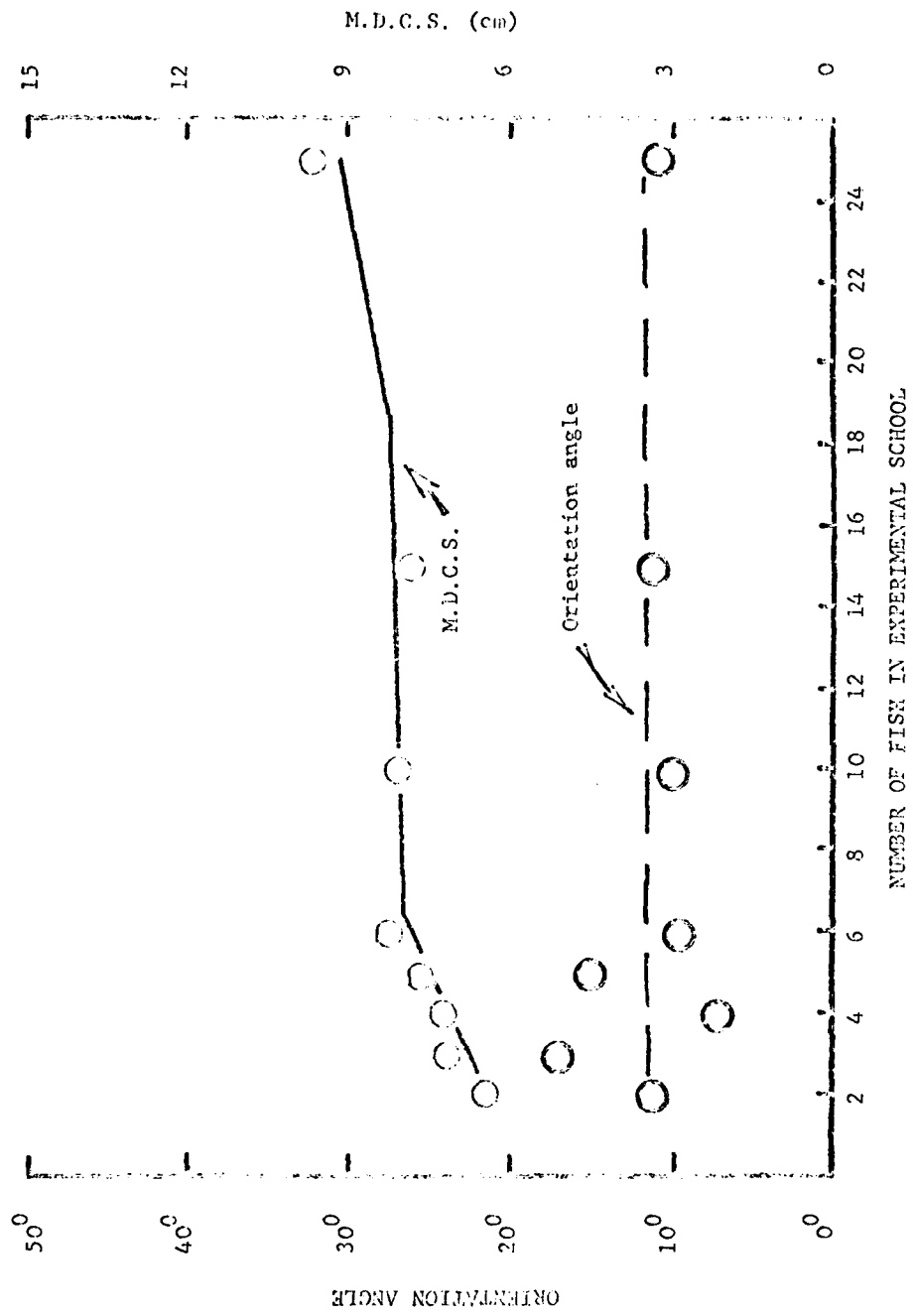


Figure 2. Effect of reduction of dissolved oxygen on school density and orientation in anchovies.

Black faced bars are two standard errors of the mean. Water temperature varied from 19.0 to 20.7°C; pH varied from 8.05 to 8.10. At conclusion of the experiment all fish showed signs of distress but none were dead. The middle graph represents the decline in oxygen produced by gassing the reservoir tank slowly with nitrogen.

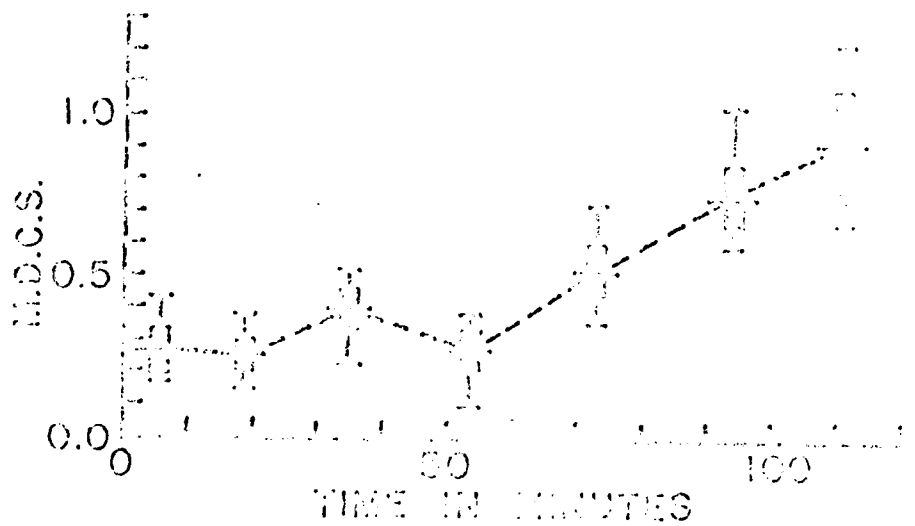
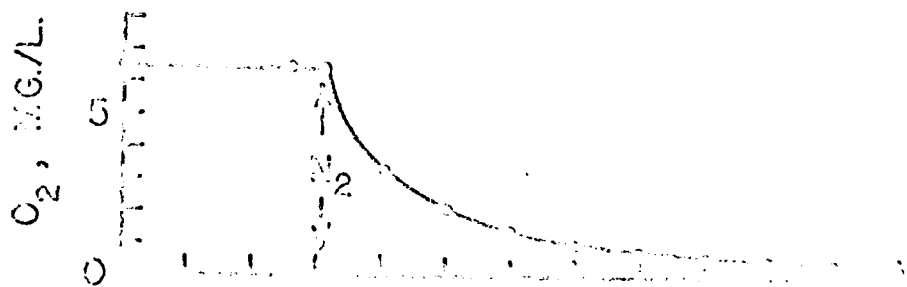
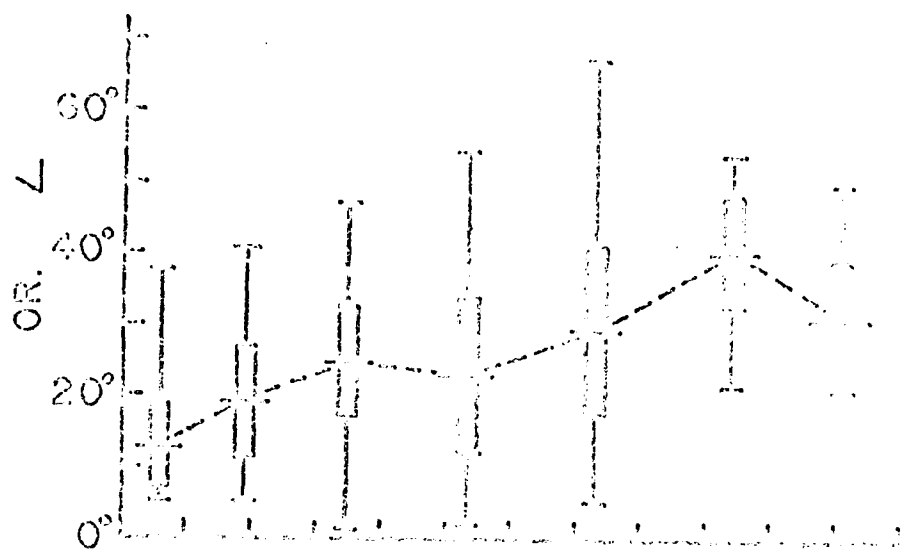


Figure 3. Effects of increased carbon dioxide on school density and orientation in anchovies.

Symbols as in Figure 2. Water temperature varied from 19.8° to 21.3°C ; oxygen varied between 6.2 and 6.4 mg/l. At conclusion of the experiment most fish showed signs of distress but none were dead. The middle graph represents the decline in pH. The decline was produced by gassing the reservoir tank intermittantly with CO_2 as indicated by the arrows.

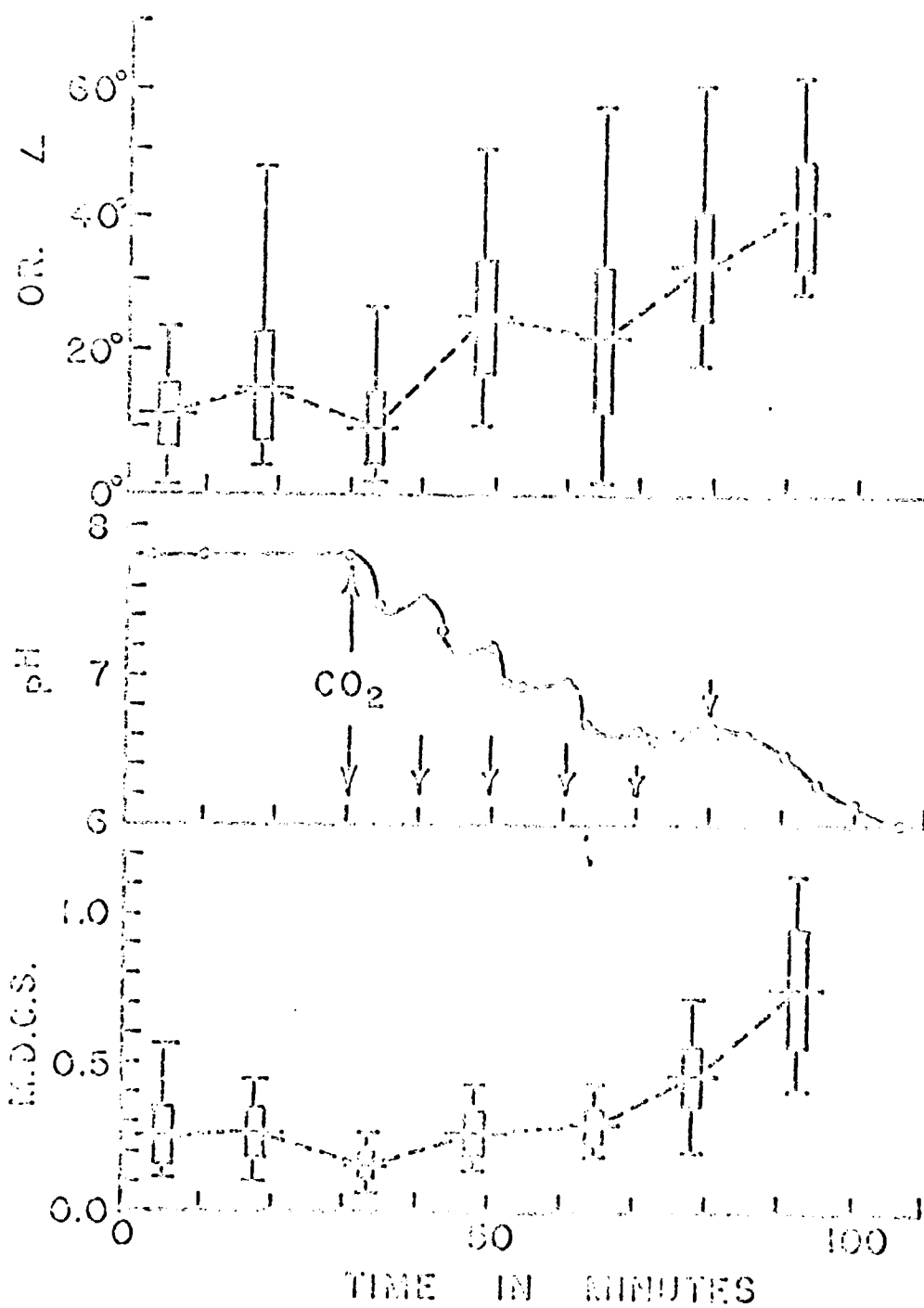
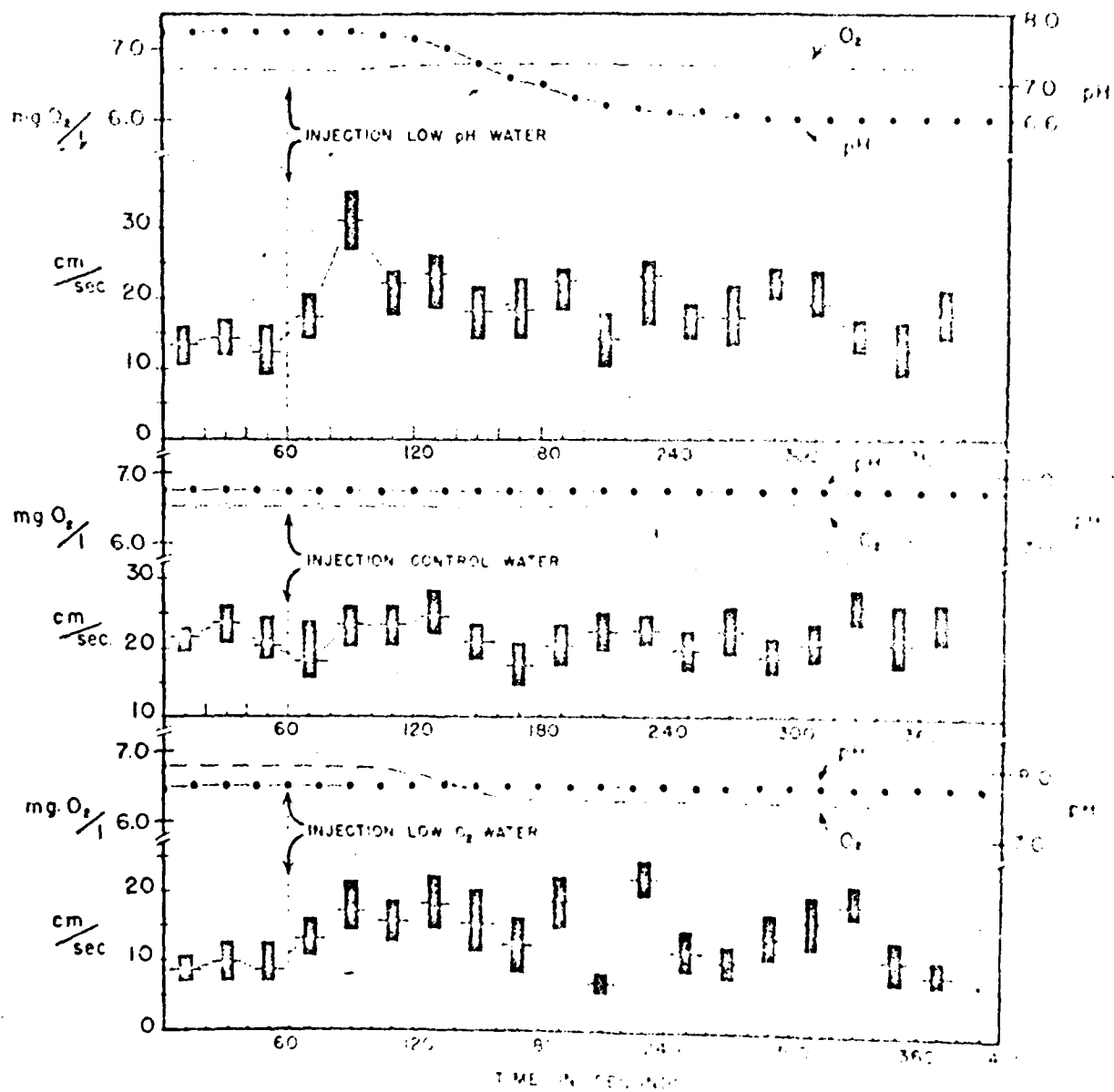


Figure 4. The effect of acute changes in oxygen and carbon dioxide on swimming velocity of anchovies.

Black bars represent two standard errors of the mean of school velocity averaged over 20-second intervals. The initial minute represents a control period where no changes were introduced from the reservoir tank. The middle graph represents a control experiment where water was injected in which oxygen or carbon dioxide levels were not altered.



Internal Behavior in Fish Schools

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Internal Behavior in Fish Schools

Abstract. *Structural changes within fish schools correlate with declines in environmental oxygen. The changes may result from the responses of individual fish to the environmental consequences of group metabolism. Individual behaviors are adaptive to the school in that they tend to maintain stability between school members and their environment.*

During late fall in North America striped mullet, *Mugil cephalus*, form dense reproductive schools and migrate from bays of the Gulf Coast and southern portions of the eastern seaboard into the open sea. The mullet are large (20 to 40 cm), often school at the surface, and usually must migrate through passes into the ocean, extended observation of school structure is possible. We have accumulated data on types of schools and their alterations. When viewed from above the schools resemble geometric figures, such as circles, discs, ellipses, triangles, wedges, crescents, and lines. Internal structure is often modified within seconds or minutes, causing school shape to change in a kaleidoscopic fashion. Normally the schools are composed of a large proportion of polarized individuals. Change in school shape may or may not involve disruption of this parallel orientation, but if it does, disruptions are transient or localized within areas of the school. Individual members of a school continually exchange positions through slight alterations of swimming speed or direction even if school shape is not altered. Similar behaviors have been noted in other schooling species (see 1-5).

Several factors may cause school structure to change. Nonenvironmental

factors, such as variation in individual tendencies to associate or disassociate, could result in the described group behaviors. The importance of these and other innate tendencies are difficult to assess. Environmental factors that might operate include temperature, light, salinity, water currents and waves, predation, feeding, bottom topography, and water chemistry. Of these factors we believe that levels of temperature, light, salinity, and water movement are too homogeneous in marine environments to be responsible for the continuous changes observed in behavior. School structure changes in response to acute predation but it is usually recognizable as a radiating eruption of portions of the school from the water surface (2). It bears no resemblance to the slower and continuous modifications of school structure described here. The constant shifting in position of individuals within mullet schools, however, could function in feeding. Positional shifts would place fish in a forward and, presumably, a favorable position for feeding even if the position were maintained for only short periods. But it seems unlikely that all of the school shapes and transitions observed can be solely ascribed to feeding behavior. Examination of the stomach contents of 20 mullet taken from migrating schools

in November 1966 revealed that these fish had not been actively feeding for some time before being caught. In general, striped mullet feed in loosely associated groups and not just before spawning (3).

The most obvious chemical factors that may be involved include soluble gases and dissolved organic substances of inter- or intraspecific origin. Of these factors only respiratory gases (oxygen and carbon dioxide), dissolved substances such as organic wastes, and perhaps specific organic secretions (pheromones) of intraspecific origin seem likely candidates. Only the respiratory gases, however, can be easily and rapidly analyzed in the field.

If we assume that respiratory gases may effect certain changes or characteristic "postures" in school structure, then the following sequence of events may take place. Reduction of dissolved oxygen and increase of carbon dioxide from school metabolism may be sensed by individual fish. This detection of altered environmental-gas concentration could induce modified behaviors such as changes in direction (orientation), spacing, and swimming velocity. The overall result would be the observed tendency toward continuous variability in group behavior. This hypothesis implies that individual physiological and behavioral response is transferred into social behavior in such a manner that it shortens the exposure of individual fish to less favorable conditions (low oxygen, high carbon dioxide and low pH, or both). In-

School	Longest dimension (m)	O ₂ (mg/liter)		Oxygen reduction (%)
		Out-side	In-side	
<i>Small schools</i>				
a*	4	6.80	6.50	4.4
b	7	7.20	6.95	3.5
c	9	7.20	7.08	1.7
d	4	7.60	7.20	5.3
<i>Medium schools</i>				
e*	18	7.12	6.36	10.7
f	15	7.70	6.90	10.4
g	30	7.40	6.85	7.4
h	30	7.00	6.50	7.2
<i>Large schools</i>				
i†	150	7.30	5.20	28.8
j†	75	7.70	7.00	9.1
k†	240	8.00	6.70	16.3
l	300	7.60	6.00	21.0

dividual responses would function to distribute or average the effects of group metabolism to all members of the school. According to this metabolic model of the fish school, gradients of respiratory gases should exist in the water with increased changes associated with increased size and with increased density of schools.

The metabolic effect of a variety of different types of striped mullet schools expressed as the percent reduction of environmental oxygen is presented in Table 1. Reduction of environmental oxygen was detectable within all schools and correlates with school size, large schools producing greater reductions. Although a reduction in oxygen perhaps should be expected, its magnitude and its gross correlation with school size are surprising.

oxide on the environment is far less dramatic than the effect of oxygen, due to the high buffer capacity of sea water. In all instances where pH was measured, changes were not detectable, except for one large school measured on 20 November 1965 (j, Table 1). The pH decline did not exceed 0.02 units and was, in fact, only detectable as a definite and reproducible downward deflection of the meter needle upon entry into the school. We have calculated a theoretical pH decline based on the environmental oxygen reduction of 9.1 percent and an assumed average respiratory quotient of 0.8 for a school of mullet. The expected environmental pH decline was obtained from a direct carbon dioxide titration procedure which relates pH decline to carbon dioxide added (7). The calculation yields an expected change of 0.025 pH units, a value in excellent agreement with our field measurements. It is unusual, therefore, that slightly greater pH changes were not detected within the larger schools of mullet where oxygen reductions were higher (i and k, Table 1), but this may have been due to the limitations of our equipment. Our results do

It is possible to ascribe many of the observable changes in schools and even specific types of structures (varied shapes, spacing, and the like) to the effect of school metabolism. These behaviors may be adaptive in that they lessen the metabolic impact of the school on individual members of the group. However, it is difficult to demonstrate that the intensity of school metabolism is actually sufficient to modify school structure. Demonstrations of exactly how group metabolism might affect structure is even more difficult. And, even if a given school shape, spacing among fish, or a change in structure lessened the effects of group metabolism on individuals, the behavior could result from nonmetabolic as well as metabolic causes. In this case a direct correlation between metabolism and structure could not be demonstrated since a direct cause and effect relationship would not exist.

TIME 1609

5.1

6.1

PH 8.2

150 m.

5.9 6.7 6.1 5.8 5.4 5.2 5.9 5.6 5.4 5.5 5.9 6.2 6.5 5.5 6.2 6.8 7.0 7.0 6.6 6.4 7.3 7.2 7.4 7.2 6.5

NET DIRECTION SCHOOL

SLOW INCOMING CURRENT

PH 8.2

WATER DEPTH IN SCHOOL..... 60-120 cm.

O₂ 7.3 30 7.3 30 7.2

TIME - 1620 1610 1600

ELECTRODE DEPTH (cm)

PH 8.2

NOV. 28, 1964

2

school structure. The most dramatic example is represented in Fig. 1. Fish in the front half and along the sides of the school were dense and highly polarized. Toward the center the fish were less polarized and swam slowly in various directions. In the back one-third of the school the fish were extremely dense, often in actual contact, completely unpolarized, and actively roiling the surface of the water. Individual fish appeared to rise to the surface and then retreat below. This activity constantly mixed the entire rear of the school, producing a turnover in the position of its members. Oxygen reductions of 22.6, 24.7, and 28.8 percent were obtained from three traverses through the school. In each instance the oxygen declined abruptly rather than gradually from the front to the back of the school. When we had completed the first oxygen profile and while the electrode was still at the back of the school, an unusual event took place. The entire rear portion of the school broke into several small schools and swam off in several directions (see inset, Fig. 1). While most of these small schools rejoined the large school during the next few minutes, at least one group did not. We conclude that the disruption of school behavior resulted from the abrupt and severe metabolic reduction of environmental oxygen and also an increase in the amount of carbon dioxide or, at least, from some undetected consequence of this metabolism [possibly release of a substance akin to "schreckstoff" (8)]. Avoidance of low oxygen has been demonstrated, however, for a number of species of fish (9). Field tests reveal that school-

ing alewives (*Alosa pseudoharengus*), when presented with a choice, consistently enter water with the least free carbon dioxide, if the difference presented exceeds 0.3 part per million (10). While these results do not conclusively demonstrate that the behavior of fish can be influenced by reasonably small gradients of respiratory gas concentrations, the results are consistent with our hypothesis. Not all structural changes in the school can be expected to result from group metabolic effects. For example, the constant slow interchange of position between individual fish in mullet schools is probably not caused by the effects of group metabolism, although metabolic effects may enhance the rate of interchange. That the interchanges are not the result of group metabolism is shown by the experimental demonstration that isolated schooling fish alter position relative to a moving visual field even though orientation to general movement of the field is maintained (5). This seems to represent an innate optomotor response which may be species specific. One functional result of this type of behavior is school turnover or mixing. We consider interchange adaptive, perhaps preadaptive to the formation of large dense schools, in the sense that it acts to equalize the time of exposure of each member of a school to the full metabolic impact of the group.

Whether the hypothesis may be generalized to other species must be demonstrated. It seems reasonable to expect, however, that dense schooling species as represented by many herrings and anchovies must change environmental gases through group metabolism. It is important in this regard that the hy-

pothesis suggested here was first formulated from our limited observations of the behavior of small schools of the northern anchovy, *Engraulis mordax*, and not from our study of striped mullet.

Position within a school can expose a fish to a considerable reduction in oxygen. This condition can alter the physiology and behavior of a fish so that its chance for survival, relative to other members of the school, may be diminished if corrective action is not taken.

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13. ABSTRACT Both field and laboratory-experimental data are presented to support a hypothesis relating group metabolism of fish schools to changes in school behavior. Specifically, it is shown that large schools of <u>Mugil cephalus</u> cause dramatic decline in environmental oxygen levels. These changes if sufficiently large are postulated to modify school behavior. Experimental manipulation of either oxygen or carbon dioxide is shown to have little effect on school behavior if the changes occur slowly. More rapid changes do not alter school structure, but do cause schools to avoid such changes. The means by which this may be accomplished and how it is transferred to group action is discussed.			

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14. KEY WORDS	LINK A		LINK B		LINK C	
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